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Shell Growth of *Mytilus trossulus* Gould, 1850, in Port Valdez, Alaska

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Abstract. Shell growth of intertidal *Mytilus trossulus* in Port Valdez, Alaska, site of a marine oil terminal, is assessed using descriptive methods and the Gompertz growth model. Age-frequency data indicated that mussels of the young to middle age classes (age classes 1 to 5) were dominant in the mussel beds, and individuals older than 7 years were not common. Percentages of new shell growth calculated by month indicated that most new shell growth occurred during the summer with no growth during winter. Growth was greatest for younger mussels with only a little new shell growth for mussels in age class 7 and above. Gompertz growth curves demonstrated differences between sites within Port Valdez related to environmental differences. The addition of a seasonal component to the Gompertz models indicated a strong seasonal amplitude to growth with maximum growth rates estimated to occur during the month of June. Comparisons of curve parameters indicated reduced growth relative to studies from lower latitudes. It is concluded that mussels in Port Valdez are stressed by exposure to natural environmental extremes in the intertidal region resulting in decreased growth.

INTRODUCTION

Shell growth of *Mytilus* species has been extensively documented under a variety of natural and laboratory conditions, and the general factors controlling this growth are well described (see review by Seed & Suchanek, 1992). It is generally accepted that the timing of growth cycles in mussels is influenced by seasonal temperature ranges and the availability of food resources (Seed & Suchanek, 1992). In addition to temperature and food availability, important factors influencing shell growth include wave exposure and salinity. While exposure to environmental contaminants can adversely affect shell growth in *Mytilus* (e.g., Stromgren et al., 1986), variability in growth, as a response to natural environmental factors, may mask sublethal impacts on mussels (Seed & Suchanek, 1992). Thus, studies assessing the response of mussels to environmental contaminants have not focused on shell growth alone.

Port Valdez, a subarctic fjord in the northeastern corner of Prince William Sound, Alaska, is the site of the marine oil terminal serving as the terminus of the Trans-Alaska pipeline. Recent evidence indicates that the mussel in Port Valdez is *Mytilus trossulus* Gould, 1850, rather than *M. edulis* Linnaeus, 1758, as previously believed (e.g., McDonald et al., 1991; see also Blanchard & Feder, 1997). Some aspects of the biology of *M. trossulus* from Port Valdez were reported by Feder & Keiser (1980) who suggested that the period of peak shell growth follows the onset of spawning in late spring. Monitoring studies relative to the marine terminal include investigations of the ecology of *M. trossulus* (see review in Shaw & Hameedi, 1988). For example, Blanchard & Feder (1997)

summarized the findings of reproductive studies of intertidal mussels from Port Valdez. This paper describes shell growth of intertidal *M. trossulus* from Port Valdez, Alaska, at sites within and remote from the boundaries of the marine oil terminal.

METHODS

The Study Area

The study reported here assesses intertidal mussel populations at three sites in Port Valdez, Alaska: Berth 4 (B4, within the confines of the Alyeska Marine Terminal), Sawmill Spit, (SS, a short distance west of B4 and outside of the marine terminal boundaries), and at Mineral Creek (MC, across the port from B4) from January 1981 to September 1982 (Figure 1). These sites were among those considered in the reproductive study of Blanchard & Feder (1997). The tidal range is approximately 6 m (Colonell, 1980). The annual air temperature in Port Valdez ranges from approximately −10°C to 25°C, and surface water temperatures range from −2 to 16°C (Blanchard & Feder, 1997). In summer, Port Valdez exhibits a positive estuarine flow with heavy sediment loads and decreased salinity (approaching 0‰) while in winter, freshwater input decreases and estuarine circulation ceases (Colonell, 1980). While all sites experience decreased salinity and increased sediment loads in summer, the MC site is most heavily affected by these physical stresses by virtue of its proximity to Mineral Creek, a glacial stream.

Sampling and Laboratory Procedures

Mussels were collected monthly at the three sites in 1981 (January–November)–1982 (January–September).
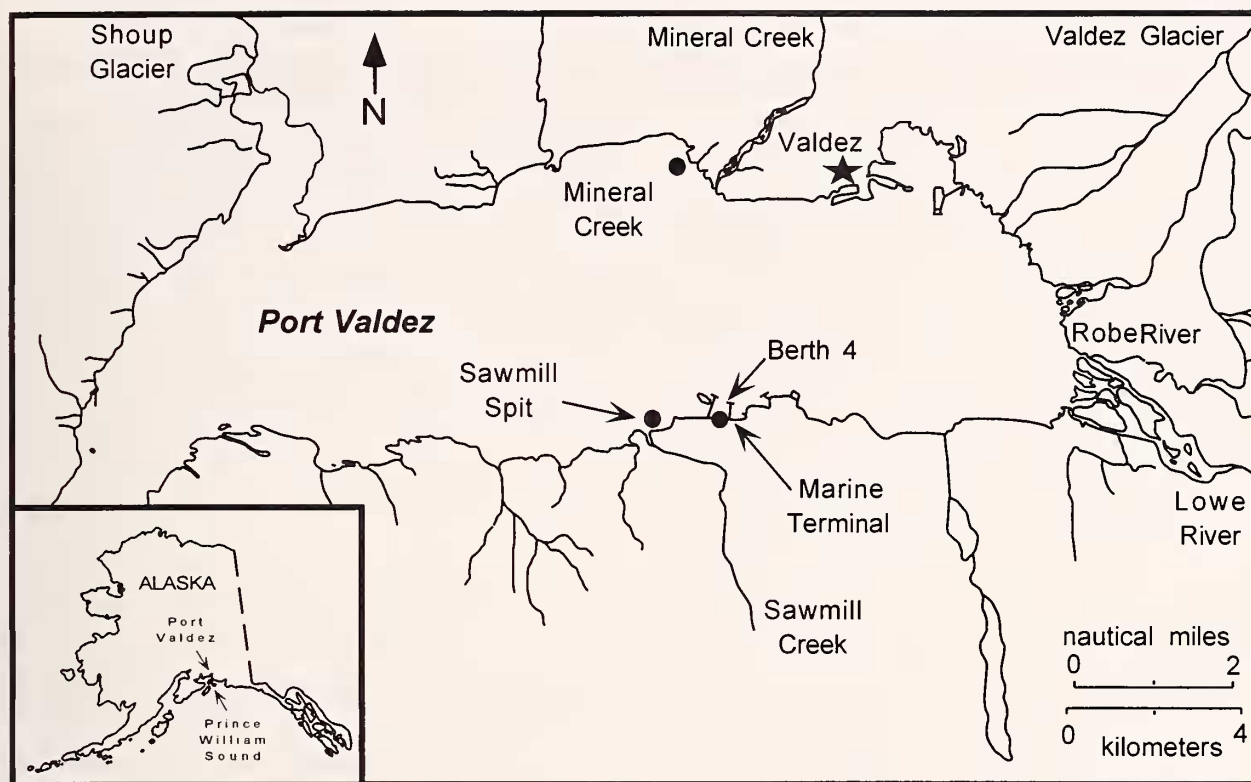
Figure 1

Map of sampling locations in Port Valdez, Alaska. Sampling locations are indicated with a large dot.

Three destructive plots were taken by randomly tossing a 0.0156 m² (12.5 × 12.5 cm) sampling frame onto the mussel bed in the mid-intertidal zone. Shells were aged in the laboratory by counting growth annuli which were readily apparent due to cessation of growth in mussels during winter in Port Valdez (Feder & Keiser, 1980). Validation of the aging technique was performed in a pilot study where the shells of 100 mussels were notched in the spring and examined 1 year later (Feder & Keiser, 1980). Observations the following year indicated that all mussels had formed a single annulus confirming the validity of annuli for use as an aging tool specifically for this Alaskan mussel population. The age of mussels in this study was estimated as the sum of observable growth rings, not including the shell edge. Total shell length, the maximum distance from the umbo to the shell edge, was measured to the nearest 0.01 mm. New shell growth was measured as the maximum distance from the last age annulus to the edge of the mussel shell. Although every effort was made to estimate the age of each mussel, specimens with shells too badly eroded to age could not be included in the determination of the age to shell-length relationships. The 0 age class referred to here applies to those individuals of the settling year class that have undergone only one partial growing season and survived through only one winter. Movement of a mussel to the next age class occurs when new shell growth can first be observed, usually in the spring of the year.

Data Analysis

Age-frequency distributions and mean shell size per age class of mussels from each site are summarized on an annual basis. The mean new shell growth and percent new shell growth for each age class by year are also presented. The percentage of new shell growth is plotted against the proportions of gametic tissues and nutritive tissues after Blanchard & Feder (1997).

Shell growth was modeled using a Gompertz growth equation. The Gompertz equation is given by:

$$L_f = L_\infty e^{-e^{-k(t-t_0)}}$$

where L_f = the length of mussel at age t, L_∞ is the asymptotic maximum growth, k = growth coefficient, t = age of mussel, and t_0 is the curve's inflection point (Ratkoskwy, 1990); this is a reparameterization of the usual Gompertz growth model applied to mussels (e.g., Seed & Suchanek, 1992). This curve is appropriate for shell growth that follows a sigmoidal curve but assumes that growth is determinate, an assumption that is often appro-

priate for slow-growing mussels (Seed & Suchanek, 1992). To account for seasonality, a seasonal component was added to the Gompertz growth model resulting in:

$$L_f = L_\infty e^{-e^{-k(t - t_0)} - \frac{CK}{2\pi}Sin[2\pi(t - t_s)]}$$

where C is the amplitude of the seasonal growth oscillation ($0 \leq C \leq 1$), t_s estimates the fraction of the year elapsing before the maximum growth rate occurs (see Sparre et al., 1989), and t_w (t_s + 0.5) indicates the time of the year when growth is minimal. The parameter C gives indication of the strength of the seasonal pattern, as values near zero suggest little change in growth over a year, while values near one indicate maximal amplitude to growth patterns. When C equals one, no growth occurs at time t_w. Based on preliminary analyses, the parameter C was fixed at one for all seasonalized Gompertz models. The age of mussels was calculated as the age estimated by growth annuli plus the fraction of the year corresponding to the month the sample was taken. For example, an age 4.5 mussel is a mussel with four growth rings collected in June (4 + 6/12). To increase the number of specimens in the older age classes, data from 1981 and 1982 were combined by site.

Growth model parameters were estimated by the nonlinear regression procedure in SYSTAT 7.0 (SPSS Inc., 1997) using the Gauss-Newton maximization algorithm with the least-squares loss function [Loss = (Observed − Expected)^2]. Since the sample size for each data set was large (n $\geq$ 3600), normal confidence intervals were calculated for each parameter (95% CI = parameter ± 1.96* Asymptotic Standard Error). Convergence, the ability of the maximization algorithm to calculate the parameter estimates, is useful to assess the fit of nonlinear models. For models that fit data well, a program will require fewer iterations to determine parameter estimates with only small changes in estimated values in the final iterations. For the Gompertz models applied here, convergence was usually gained in about 10 iterations from starting points close to the final parameter estimates. Poor convergence was noted when the number of iterations required approached 20 or more and/or parameter estimates still changed substantially in later iterations. Coincidence of growth curves was tested using a general F-statistic of the form

$$F_{(1-\alpha, 2(k-1), DF_p)} = [(SS_t - SS_p)/2(k - 1)]/[SS_p/DF_p]$$

where SS_t = sum of squares for the single regression line for all populations combined, SS_p = the sum of SS for regression lines fit to individual populations, k = number of populations compared, and Df_p = degrees of freedom of SS_p (Zar, 1996). If the F-statistic is not significant, this indicates that a single growth curve is adequate to describe the populations compared. Tests of coincident growth curves (performed only for the normal Gompertz growth models) were made first for all sites combined

Table 1

Age-class distribution (ind. 0.047 m^{-2}) of *Mytilus trossulus* by site and year.

Age	B4-81 No.	B4-82 No.	MC-81 No.	MC-82 No.	SS-81 No.	SS-82 No.
0	268	128	12	428	75	124
1	325	185	32	634	145	209
2	1345	644	354	130	554	216
3	402	667	1039	292	670	318
4	238	150	387	575	345	515
5	233	55	163	245	154	201
6	175	41	71	77	67	31
7	42	39	27	45	30	19
8	8	9	7	15	4	3
9	5	0	2	9	1	
10	1	1	1	5		
11				1		
12				0		
13				1		
Total	3042	1919	2095	2457	2045	1636

and then, if the first F-statistic was significant, between pairs of sites.

RESULTS

The age-frequency distributions for mussels from the study sites indicated a dominance of young mussels (Table 1). Age class 0 mussels did not occur in large numbers. The minimum count for this age class was 12 mussels 0.047 m^{-2} in 1981, and the maximum was 428 mussels 0.047 m^{-2} in 1982, all at the MC site. Mussels in age classes 1–3 were the most abundant, and the first six age classes (age 0 to 5) generally comprised over 90% of the individuals present at all sites. Mussels older than 7 years of age were relatively uncommon. It was only at the MC site that mussels older than 10 years occurred. The minimum length observed was for an age 0 mussel of length 0.49 mm at the B4 site, and the maximum was 58.00 mm for an 8-year-old mussel at SS.

Assessment of shell growth by age class indicates that the highest percentage of new shell growth occurs within the younger age classes with only a small percentage of new growth added after age 6 (Tables 2, 3, and 4). The new shell growth of mussels can represent over 50% of mean shell length for age class 1 mussels. Shell growth does not occur during winter months, from December to February, and remains minimal through March (Figure 2). The percentage of new shell growth per month increases greatly in May, and maximum growth rates, apparent as the steepest portions of the lines in the plots of % new shell growth, occur from June to August.

The normal and seasonalized Gompertz growth models revealed some differences between sites (Figure 3). Convergence of the normal Gompertz models was excellent,

Table 2

Mean length and standard error (SE) of *Mytilus trossulus* in each age class by site and year. N/A = not available due to either no mussels or a single mussel in an age class.

Age	B4-81		B4-82		MC-81		MC-82		SS-81		SS-82	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
0	2.54	0.06	2.01	0.09	2.90	0.18	2.33	0.04	2.91	0.16	2.23	0.13
1	6.79	0.21	5.35	0.26	8.45	0.63	3.20	0.07	7.16	0.29	5.63	0.17
2	14.89	0.17	11.87	0.23	14.49	0.30	9.29	0.32	13.81	0.30	12.18	0.38
3	21.79	0.35	24.06	0.28	18.89	0.20	18.80	0.29	23.85	0.30	21.84	0.43
4	28.85	0.45	30.76	0.51	28.80	0.34	24.16	0.20	26.95	0.46	29.48	0.28
5	35.10	0.36	33.78	0.72	34.78	0.39	31.84	0.31	31.12	0.69	35.00	0.36
6	38.15	0.37	37.28	0.65	37.85	0.56	36.73	0.52	36.29	1.01	38.57	0.72
7	38.24	0.64	39.01	0.67	40.49	0.77	38.90	0.70	40.83	1.05	40.35	1.26
8	40.13	2.39	37.70	1.20	40.59	1.25	40.59	1.13	45.04	4.58	43.23	2.05
9	39.44	1.00	N/A	N/A	46.67	2.25	43.54	1.09	46.81	N/A		
10	44.82	N/A	35.12	N/A	48.75	N/A	40.55	1.83				
11							40.38	N/A				
12							N/A	N/A				
13							37.50	N/A				

but convergence of the seasonalized models was poorer, particularly for the SS site. Tests for coincidence of growth curves between sites were all highly significant ($p < 0.0001$) indicating that a curve for each site was necessary to estimate the normal growth models. Comparison of the 95% confidence intervals of parameter estimates between each site (Table 5) indicated that model estimates for the MC site were significantly different than the B4 and SS sites (observed as no overlap of the 95% confidence intervals), while the values of the B4 and SS sites were not different (i.e., overlap of confidence intervals for each parameter). A poor fit of the growth curves for age 0 mussels (Figure 3) is apparent as the mean lengths of age class 0 mussels from January to April (age

< 0.4) was greater than the values estimated in the growth curves. Since movement into the next age class is marked by new shell growth, first visible in the spring, the age 0 mussels occurring in the first of the year (January through April) are those approaching the period of new shell growth and their movement into the next age class.

The seasonalized Gompertz model provides an estimate of two additional parameters, C and t_s, useful for assessing growth patterns. The amplitude of the seasonal component estimated by the parameter C, here fixed at one based on preliminary analyses, indicates high amplitude seasonal growth patterns and suggests that no growth occurs during the period estimated by t_w ($t_w = t_s + 0.5$).

Table 3

Mean (mm) new shell growth and standard error (SE) of *Mytilus trossulus* in each age class by year and by station. N/A = not available due to either no mussels or a single mussel in an age class.

Age	B4-81		B4-82		MC-81		MC-82		SS-81		SS-82	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1	3.94	0.17	3.32	0.20	5.72	0.47	1.87	0.06	4.25	0.23	3.66	0.15
2	6.32	0.12	4.28	0.17	6.18	0.24	2.34	0.23	5.70	0.20	4.71	0.29
3	6.09	0.22	4.93	0.19	4.82	0.14	2.26	0.17	5.73	0.15	2.96	0.20
4	4.32	0.23	3.21	0.27	4.08	0.17	2.77	0.10	3.58	0.19	3.45	0.11
5	3.08	0.16	1.38	0.27	2.00	0.16	2.32	0.14	2.25	0.18	2.32	0.15
6	1.98	0.13	0.97	0.16	1.18	0.15	1.45	0.14	1.41	0.18	1.28	0.25
7	1.08	0.22	0.64	0.11	1.08	0.27	1.23	0.20	0.93	0.16	1.10	0.25
8	0.91	0.29	0.29	0.13	1.55	0.40	0.58	0.14	0.66	0.14	0.50	0.31
9	0.19	0.13	N/A	N/A	1.21	0.34	0.51	0.11	0.59	N/A		
10	0.00	N/A	0.12	N/A	0.87	N/A	0.41	0.15				
11							0.16	N/A				
12							N/A	N/A				
13							0.20	N/A				

Table 4

Percent new shell growth (of total length) of *Mytilus trossulus* in each age class by year and by station. N/A = not available due to either no mussels or a single mussel in an age class.

Age	B4-81 %	B4-82 %	MC-81 %	MC-82 %	SS-81 %	SS-82 %
1	57.95	62.09	67.74	58.54	59.30	65.00
2	42.48	36.07	42.61	25.17	41.31	38.70
3	27.94	20.48	25.52	12.04	24.01	13.54
4	14.98	10.44	14.16	11.45	13.28	11.71
5	8.77	4.10	5.76	7.30	7.22	6.64
6	5.20	2.60	3.11	3.94	3.88	3.31
7	2.82	1.64	2.67	3.17	2.27	2.73
8	2.26	0.78	3.82	1.44	1.47	1.16
9	0.49	N/A	2.58	1.17	1.26	
10	0.00	0.34	1.78	1.01		
11				0.40		
12				N/A		
13				0.53		

The t_s coefficients indicate that 49% to 53% of the year elapses before growth rates reach maximum values corresponding to the month of June and thus, t_w corresponds to January.

DISCUSSION

Mytilus trossulus in Port Valdez demonstrates shell growth patterns comparable to growth of *Mytilus* from Greenland (e.g., Theisen, 1973). Theisen (1973) considered mussels in Greenland to be *M. edulis,* but based on current knowledge, those mussels could be either *M. edulis* or *M. trossulus* (Gosling, 1992). Relative to the growth of mussels from the intertidal samples reported by Theisen (1973), mean shell lengths of 3 to 4 mm are recorded for mussels of age class 1 (as determined by applying our aging technique to his growth check data), 30 to 36 mm for mussels for 6-year-old mussels, and 42 to 52 mm for 9-year-old mussels. Lengths of the first few age classes of the present study (e.g., age 0–3 mussels; Table 1) are greater than those from the Theisen (1973) study, but mean lengths of mussels after the sixth year are similar. Intertidal mussels of Theisen (1973) demonstrated life spans similar to those observed in this study (up to 12–13 years), and younger mussels were dominant in the Greenland samples as well, with mussels >7–8 years of age relatively uncommon. The range of maximum length of mussels estimated by the Gompertz model from sites in Port Valdez (41.0 to 44.3 mm) is less than those estimated by Theisen (1973) (54.9 to 62.5 mm). Unlike the present study where the Gompertz model fit all age classes relatively well, Theisen concluded that the von Bertalanffy growth equation fit his data better for older mussels, while the Gompertz equation was better

for the younger mussels. The differences in model fitting and the estimated maximum lengths may be due to the varying methodologies (the Ford-Walford plot method vs. nonlinear regression) or possibly to genetic differences in growth between *M. trossulus* and *M. edulis.*

Decreased temperature and salinity are known to result in reduced growth in mussels (Seed & Suchanek, 1992). Theisen (1973) reported reduced shell growth of mussels from Greenland, as compared to populations at lower latitudes, and related reduced shell growth to low temperatures within his study area. Tedengren & Kautsky (1986) concluded that the reduced growth of Baltic Sea mussels (now considered to be *M. trossulus;* Gosling, 1992), compared to mussels from the North Sea, resulted from physiological adjustments to low salinity (from 4.5 to 10%—similar to conditions in Port Valdez in summer). Thus, shell lengths of mussels from Port Valdez may be reflective of seasonal environmental stress. Natural sources of stress at the study sites in Port Valdez include high sediment loads (ranging up to 100 mg L^{-1}; Sharma & Burbank, 1973) and decreased salinity (approaching 0‰; Blanchard & Feder, 1997) in summer, and freezing air temperature in winter, as well as year-round low water temperatures. However, to fully understand the effects of decreased temperature and salinity on shell growth of *M. trossulus* in Port Valdez and along the Pacific coast, experimental studies similar to those performed for *M. edulis* are necessary (e.g., see review by Seed & Suchanek, 1992).

The seasonal growth pattern in mussels from Port Valdez reflects the subarctic climate at this fjord. In summer, the length of daylight approaches a maximum of 20 hours while in winter, from mid November to early February, there are less than 7 hours (Alexander & Chapman, 1980). Phytoplankton abundance increases in early spring, as daylight increases, reaching maximum levels in May and June (Alexander & Chapman, 1980). A minor phytoplankton bloom occurs in fall, but low abundance levels are reached by November and continue through the winter. Consequently, shell growth in *Mytilus* is minimal in spring, increases rapidly in mid-summer once gamete maturation is completed and spawning initiated, and ceases in winter (Feder & Keiser, 1980; Blanchard & Feder, 1997). This seasonal growth pattern is indicated by the plots of % new shell growth (Figure 2) and the seasonalized Gompertz growth models (Figure 3).

Due to the response of shell growth to varying conditions in field studies, it may be impossible to discriminate any sublethal effects of contaminants from natural environmental variations. Studies attempting to assess effects of contaminants on *Mytilus* generally rely on assessment of other aspects of mussel biology. Blanchard & Feder (1997) investigated the reproductive and nutritive storage tissue cycles for *M. trossulus* in Port Valdez including the sites of the present study. They found that mussels at the MC site demonstrated significantly less reproductive tis-
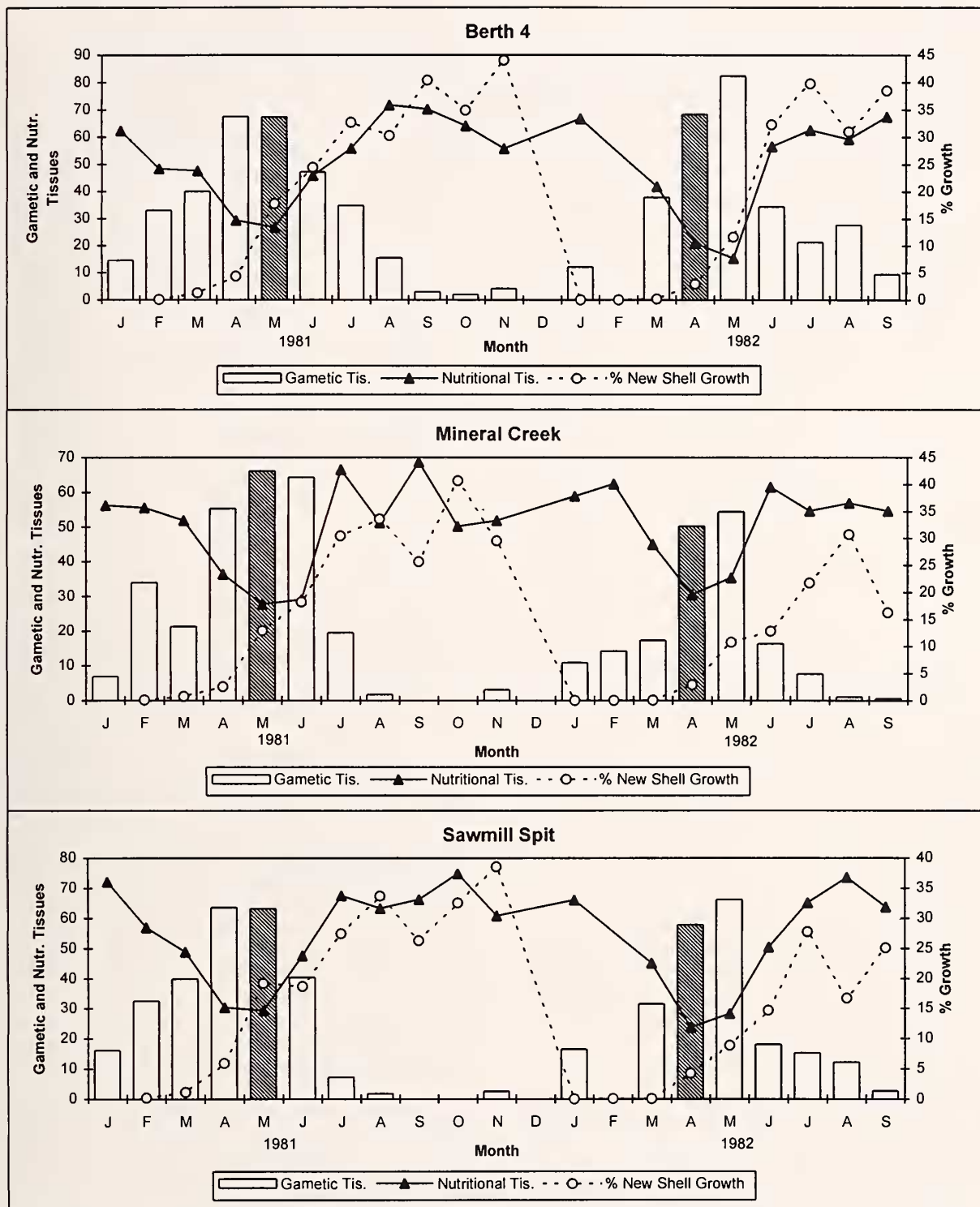
Figure 2

Bar charts of proportions of gametic tissue overlain by proportions of nutritive tissues (data from Blanchard & Feder, 1997) and percent new shell growth for *Mytilus trossulus* from Port Valdez in 1981 and 1982. Filled bars indicate the first occurrence of appreciable amounts of reproductive tissues in spawning condition.

Table 5

Parameter values and 95% confidence intervals for Gompertz growth models. L_∞ = maximum length, k = growth coefficient, t_0 = length at time = 0, and t_s = fraction of year before maximum growth rate. ASE = asymptotic standard error. N/A = not available.

Site	Parameter	Parameter estimate	ASE	95% Confidence intervals Lower bound	95% Confidence intervals Upper bound
B4	L_∞	40.98	0.404	40.18	41.77
	k	0.668	0.015	0.639	0.696
	t_0	2.651	0.019	2.614	2.688
Seasonal Model	L_∞	41.28	0.395	40.51	42.06
	k	0.664	0.014	0.637	0.692
	t_0	2.694	0.019	2.656	2.732
	t_s	0.491	0.017	0.459	0.524
MC	L_∞	44.30	0.558	43.21	45.40
	k	0.511	0.011	0.490	0.532
	t_0	3.131	0.030	3.072	3.190
Seasonal Model	L_∞	43.74	0.525	42.71	44.77
	k	0.525	0.011	0.504	0.546
	t_0	3.079	0.029	3.023	3.135
	t_s	0.533	0.017	0.500	0.566
SS	L_∞	41.55	0.693	40.19	42.91
	k	0.608	0.020	0.569	0.647
	t_0	2.731	0.034	2.664	2.797
Seasonal Model*	L_∞	42.26	N/A	N/A	N/A
	k	0.605	N/A	N/A	N/A
	t_0	2.788	N/A	N/A	N/A
	t_s	0.508	N/A	N/A	N/A

* Convergence of this growth curve was particularly poor so standard errors and confidence intervals are not presented. The parameter estimates should be considered as approximate values.

sue than did the B4 and SS sites and suggested that mussels at the MC site were negatively influenced by the colder, silt-laden waters of Mineral Creek. They further concluded that effects of hydrocarbon contamination, derived from small spills and industrial activities in the terminal area, were not apparent in the reproductive cycle of mussels from Port Valdez. Similarly, the growth curves presented here revealed no differences that could be clearly related to the proximity of mussels at B4, within the terminal area, to hydrocarbon contamination. The overlap of the 95% confidence intervals of curve parameters for the B4 and SS sites indicates that although the curves for the two populations are not coincident (i.e., the F-statistic was significant), the curves are still very similar. The significant differences in parameter estimates between the curve for the MC sites and the curves for B4 and SS sites, are suggestive of environmental differences between the MC site on the northern shore and the B4 and SS sites on the southern shore of Port Valdez.

Additional conclusions can be drawn from the age-frequency distributions. Recruitment by young-of-the-year mussels was originally thought to occur by secondary settlement into the mussel beds, but recent evidence indicates that these juveniles may also settle directly into the beds (McGrath et al., 1988; Seed & Suchanek, 1992).

Feder & Keiser (1980) observed that newly settling mussels (early plantigrade stage, < 0.4 mm; Seed & Suchanek, 1992) in Port Valdez generally settled on filamentous algae and then moved into the mussel beds. All age 0 mussels in the present study were larger than the early plantigrade stage suggesting initial settlement outside of mussel beds. Additionally, the typically low numbers of age 0 mussels and large numbers of age classes 1 and 2 mussels support the secondary settlement hypothesis of Feder & Keiser (1980). While direct recruitment into the mussel beds was not observed during the 1981–1982 study, an investigation of the abundance of mussels in Port Valdez from 1989–1992 (Feder & Blanchard, 1993) indicated that large numbers of plantigrade mussels can sporadically settle directly into mussel beds (up to 2200 individuals in 0.016 m² replicates in 1990: unpublished data). Also, the age-frequency distributions indicated that the mussels in Port Valdez are generally short-lived with mussel beds dominated by mussels 5-years-old or less, and older mussels progressively more uncommon.

The findings of this study reveal a well-defined seasonal shell-growth pattern for *M. trossulus* in Port Valdez. The growth patterns of mussels reflect the extreme environmental conditions encountered within the intertidal region of Port Valdez. The seasonalized Gompertz growth
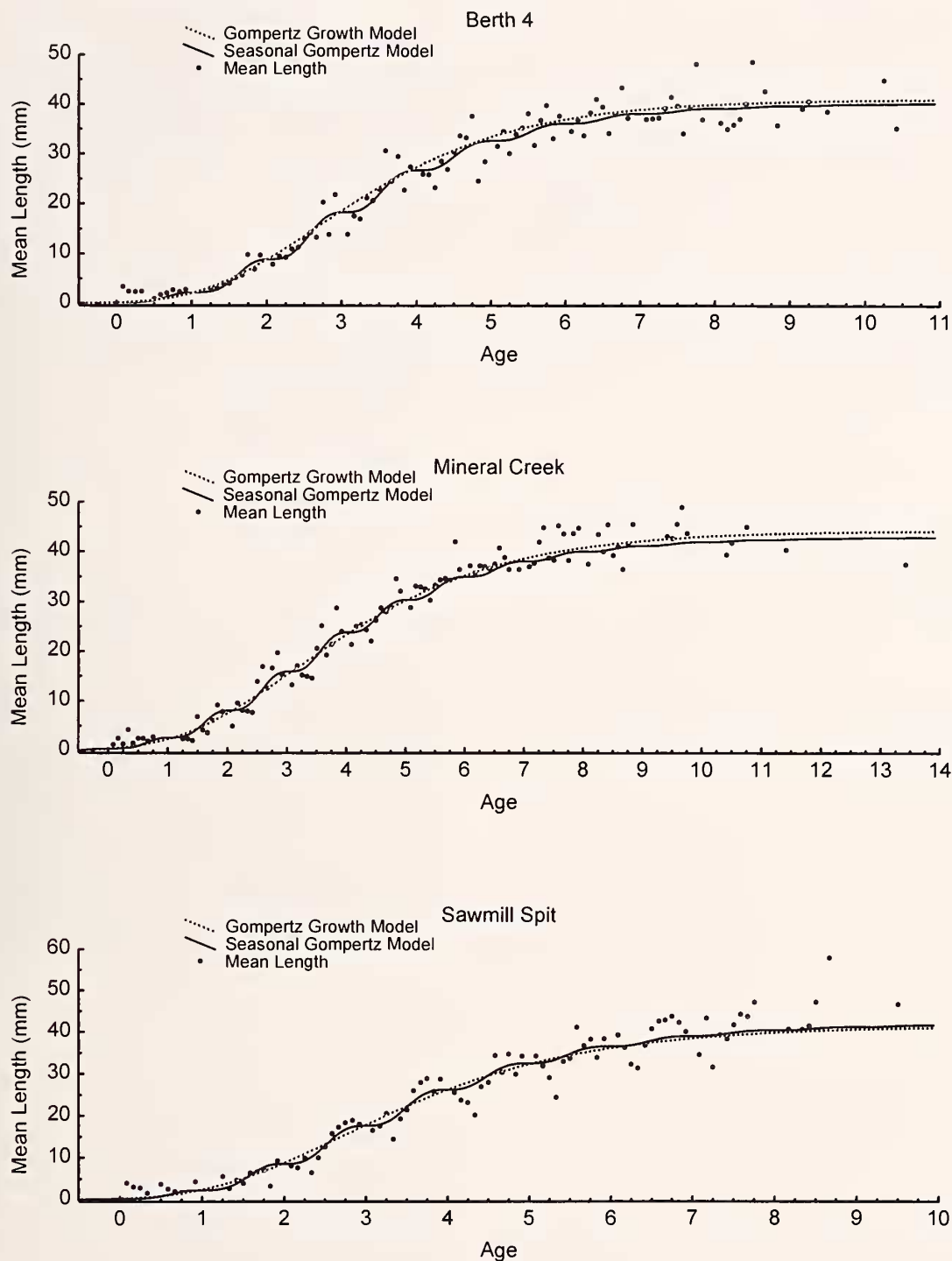
Figure 3

Gompertz growth curves and mean shell lengths for *Mytilus trossulus* from the (a) Berth 4, (b) Mineral Creek, and (c) Sawmill Spit sites in 1981–1982 from Port Valdez. Age is calculated as the sum of the observed age (by counting growth rings) and the fraction of the year in which sampling occurred. The tick marks denote fractions of a year.

curves indicate a strong seasonal component to shell growth with maximum shell growth rates during and/or after June; most growth occurs during mid summer after spawning commences. Differences in growth curves between the MC site and the B4 and SS sites are reflective of environmental differences between sites on opposite sides of the bay. Effects on shell growth due to hydrocarbon contamination were not apparent. Age-frequency distributions suggest secondary settlement of juveniles into mussel beds as the primary method for recruitment.

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